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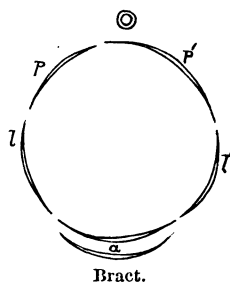
12. For the purpose of observing and recording both the imbrication of the whorl and the relation of its parts to the axis, I make a diagram of the flower (Fig. 125) and rule a table as on the opposite page (Table II) :

In this diagram of the corolla of *Pyrola elliptica* (Fig. 125) *p* and *p'* denote the upper or posterior petals ; *l* and *l'* the lateral petal ; and *a*, the anterior or lower petal.

In Table II the figures 1, 2, 3, 4, 5 represent the successive parts of the spiral. The Table shows the summing up of one hundred observations of the imbrication of the corolla of *Pyrola elliptica* Nutt.

Fig. 125.

Axis.



THE METAMORPHOSIS OF FLIES.* III.

BY DR. AUGUST WEISSMANN.

WHAT appears most unusual in the development of the Muscidæ is the genesis of the thorax and head together with their appendages. That this section of the fly's body is completely formed anew, not standing in genetic connection with the corresponding parts of the larva, contradicts the generally accepted and long prevalent view, according to which pupation is only a moulting process. As little does this opinion agree with the fact of the total transformation which all the inner organs suffer during pupation. All the systems of the organs of the larva die, in part completely, in part cell by cell, in order afterwards to be built up anew.

Evidently the metamorphosis of *Corethra* stands in diametrical opposition to this mode of development, and indeed to the two previously described main points. Here the pupation may be rightly regarded as a moulting process ; we see no phenomena de-

*Being the concluding chapter of "Die Metamorphose der *Corethra plumicornis*, ein weiterer Beitrag zur Entwicklungsgeschichte der Insecten. Von Dr. August Weissmann. Mit. 5 Kupfertafeln. Leipzig, 1866. 8vo, pp. 83.

companying the process, which cannot be brought under this head. The nature of the moulting process I see in this, that the layer of cells, which we regard as the hypodermis, and which appears as a skin split apart from the chitinous skin, after certain changes of form, develops a new chitinous skin, and that this takes place without any solution of continuity of the same. The change of form may arise merely through simple growth, accompanied by a more or less considerable remodelling; or it may be due to the formation of new, or to the disappearance of parts already present. The latter occurs through shrinkage, the former to a growing out of the hypodermis. It is the hypodermis which generally imparts to the insect its form, from which the formation of the appendages of the segments proceeds, the typical as well as the accessory.

The mere remodelling of the parts of the body already present we saw fully illustrated in the *Corethra* larva; thus the head gradually takes on a different form, the mandibles, in the young larva beset with long, slender bristles, afterward become thick, massive, raptorial jaws, with sharp teeth, etc. But most instructive are these relations in the antennæ, where indeed a less change of form, rather than a considerable increase in size may be noticed at each moult. This is accompanied, as we have seen, by a complete pushing inwards of the hypodermis, whereby is afforded in the only possible way an important space for the increase in size. After the splitting off of the old chitinous skin the stretched hypodermis-layer again turns back throughout its length and breadth. No more direct proof can be given for the correctness of the view which regards the appendages of the segments of Arthropods as protrusions of the skin.

This occurrence is only important as being a preliminary stage for the rise of the antennæ of the imago; still this arises through a simple, though still deep-reaching remodelling of the larval antennæ, and thus stands in relation with the other typical cephalic appendages. No enlargement of the parts takes place, indeed the hypodermis is simply loosened and models itself anew, for the most part during a perceptible decrease in size, into the antennæ of the imago; so for example the mandibles. But should, on the contrary, an enlargement take place, as in the under lip, then this arises through a pushing up of the hypodermis from the bottom of a falling-in of the body wall, and here the difference in size and form between the new and old organs is so considerable, that

we can rightly indeed regard it as a new formation ; the passage to the real new formation is here indicated, and we finally see also the appendages of the thorax, which in the larva are completely wanting, certainly developing in the same manner ; the simple growth of the antennæ at each moulting of the larva, the formation of the fly's beak out of the under lip of the larva, and the outgrowth of wings and limbs at places in the hypodermis previously wanting them, are also only modifications of one and the same occurrence ; the protrusion of the hypodermis.

So far it certainly appears legitimate to regard the formation of *Corethra* as a moulting process. The entire hypodermal skin it is which remodels itself, in part shortening, in part elongating and drawn out, but which never loses its continuity.

But this does happen in the *Muscidæ*. The hypodermis of the anterior larval segments must die, in order that the imaginal disks lying within the body cavity on the upper surface, and a new thorax and head may be composed ; evidently a phenomenon which exceeds the idea of a moulting. It is a mistake to exceed known facts. It were a greater error to conclude from the fact that the imaginal disks of the *Muscidæ* are already formed in the embryo, that the body of the imago was already formed, as in *Corethra*, in which the wings and limbs begin to grow after the last moulting. The imaginal disks of *Musca* are not simply rudiments of the appendages of the segments, but really *the segment itself* ; but in *Corethra* the germs of the segments of the imago are already present in the egg, not alone in the form of isolated disks, but as the complete segments of the larva, which afterwards give rise to the appendages, in order to build up the segments of the body of the adult insect. The body of the imago is also on the contrary more perfectly formed in the larva of *Corethra*.

It is by no means surprising that the appendages of the segments of *Corethra* begin to develop after the last moult of the larva. Should they arise earlier, then they would already appear during the life of the larva as external parts, the chitinous skin which in the process of moulting would separate anew would press to the half-formed appendages, and the larva would thus be no more a larva, the metamorphosis no more complete, but an incomplete one. A development of the appendages beginning *before* the last moulting would, in a metabolic insect with the mode of development of *Corethra*, be only conceivable if the same previ-

ously originated not as a direct protrusion, but as an invagination, also forming no projection on the upper surface of the hypodermis, as in fact seems to be the case in the wings of Lepidoptera.

But we will take a nearer glance at the mode in which the formation of the appendages and especially those of the thorax takes place. Many differences between *Musca* and *Corethra* appear, and also many resemblances, and indeed in points of great importance, so that we must say *that the formation of the thoracic appendages goes on in the two insects in essentially the same way, and indeed the process of formation may be considered as simply local protrusions of a broad, flat, basal membrane.* This basal membrane is in both cases the hypodermis of the thorax, which in *Corethra* at the time of formation of the appendages at once arises as a whole, while in *Musca* it exists only in a rudimentary way in the form of many pieces separated from one another. Ideally in fact the thorax of *Corethra* consists of twelve such pieces, each one of which is destined to grow out as an appendage. Only an apparent similarity lies in the relation which exists in the two Diptera between the nerves and the newly forming appendages. In *Corethra* all the appendages of the thorax, with the exception of the gills around the end of the body are provided with sensible (*sensibeln*) nerves; for then with their increasing growth the nerve-stalk will be surrounded. From the neurilemma of these nerves arises the formation of the tissues filling the cavity of the appendages; they form a store of cells (*zellzuerungen*) which are transformed into the tracheæ, muscles, sinews and nerves of the appendages. Only in the origin of the gills, the place of the nerve is supplied by a trachea, which in those organs wanting nerves and muscles certainly play the same part as the nerve.

The imaginal disks of the Muscidae also stand in connection with the nerves, but the significance of this fact in regard to the development of the appendages is still quite another thing. This is due to the fact that not *all* the disks are attached to nerve-filaments, *as indeed are not all those from which originate similar appendages.* The imaginal disks of the two anterior limbs are attached to nerves; the hinder spring up from the tracheal stems without any connection with nerves. The conclusion is inevitable that the nerve-stems are here nothing else than points of attachment for the new formations. Certainly it is evident that the nerve passes through the new formation in order to reach the

organ lying next to the skin (ganglion or muscle) ; still this is accomplished in quite a different way from the Tipulidæ, where the cavity of the appendages is traversed longitudinally by a nerve (at least in the legs), while in *Musca* the appendage is in fact wholly free from nerves, at all events with none of its primitive fibres present, and at best may be traversed by such as are formed anew during the outgrowth of the appendages. At all events the new formation of the tissues filling the cavity do not proceed from the neurilemma, but from the nuclei arising from the destruction of the fat body.

But still in the manner and mode, in which the growing limb pushes out, there is no inconsiderable difference.

In *Corethra* there is at first a completely unjointed cylindrical skin which lies wound up in a spiral on the piece of the thorax belonging to it ; as soon as the new formation has evidently grown in length, when the differentiation of the cell-masses of the cavity into tissues has advanced, the first traces of joints appear.

Quite otherwise in *Musca*, where the segmentation begins at an early period and is complete along the whole length of the projecting appendage. Even before the growth outwards of the limb ever projects up prominently above the level of the basal membrane, the end of the limb (the fifth tarsal joint), is separated from the basal membrane ; then with the elongation of the tarsal spines, the four other tarsal joints become interpolated, while the tibia and fibula still form an unjointed portion, whose complete division into the joints of the fly's limbs occurs after the formation of the thorax. During the whole development within the disk the limb still remains as a short projection which, without turning, stands straight up over its thoracic piece. As soon as the new thorax is formed, it begins to grow moderately, and considerably later, in the second half of the pupal sleep, the muscles and other tissues arise in the cavity of the appendages, and finally the limb assumes its external, definite form. From the last mentioned facts, it clearly appears that with the existence of imaginal disks, which the muscid larva brings with it out of the egg, no greater preparation in fact is made for building up the body of the imago ; that here a much more marked transformation must be undergone. When *Corethra* transforms into a pupa, the muscles of the wings and limbs are already formed, while in *Musca* there is not yet the first trace to be seen of either ; the mouth parts undergo in Co-

rethra only a final modelling, while in *Musca* the head does not yet appear as a whole, and nothing of the beak is yet formed.

But if in relation to the external form and formation of the tissues in the interior the *Corethra* larva stands nearer its imago, so not less as regards the systems of internal organs. Here also we find a complete continuity between larva and pupa; no new organs arise in place of the old, but the old either remains the same, or are wholly intact, or with only slight changes, as are required for the changed mode of life of the animal; thus the dorsal vessel passes wholly unchanged over into the fly, and except the slight shortening of the œsophageal ring, the nervous system also. Other organs are completed through increase in size in some, through concentration and disappearance in other places, as for example in the digestive canal, and the sexual organs which had long previous been completely formed. Only parts which are single become entirely superfluous and disappear and never arrive at a complete, new structure, independent of the systems of organs already present.

It is wholly otherwise in *Musca*, where all the systems of organs of the larva disappear, and are formed anew from new building materials, whether they return to molecules, which mingle with the blood, as the hypodermis of the anterior larval segments, as all the larval muscles, many of the tracheæ, the anterior part of the digestive canal; or whether they pass through that interesting process which I have termed *histolysis*, and whose nature consists in a destruction of the histological elements, without giving up the general form of the organ, and in a succeeding new formation from the ruins of the tissues.

But most remarkable and pregnant is the difference in the processes of growth within the body of the pupa, since in *Corethra* the fat bodies play throughout a very subordinate and scarcely perceptible part, while in the *Muscidæ* a building up of the inner organs without the intervention of this important part of the body were not possible. There is need only for the colossal mass of the fat body in the muscid larva; and seeing the thick whitish pap-like substance, with the product due to its destruction filling the body-cavity of the pupa, we can estimate the true significance of the fat body in the development of the *Muscidæ*. And it would appear that the fat body in these insects is not only a depot of nutritive material, but that out of the products arising from its destruction,

entirely new histological form-elements arise: the masses of nuclei which fill the body-cavity of the pupa with a compact mass, whose brood of cells, multiplying through endogenesis, arrange themselves into strings and thus form the primitive germs of the tracheæ and in fact the muscles.

Indeed it is difficult to tell out of what material the muscles of the wings of the Muscidæ should arise, if not out of the descendants of the masses of nuclei. But in *Corethra* we find the corresponding muscles already indicated in the embryo in the form of fine filaments; but how could this be the case in the Muscidæ, where the points of attachment of such filaments, the hypodermis of the thorax, are not yet present in the larva? And the same conclusion follows in regard to the tracheal system of the imago, which in *Corethra* is indicated beforehand, the entire division of the body of the imago answering to the corresponding segments of the larva—which in *Musca* can only arise when these regions are formed, *i. e.*, in the course of the pupal life.

Thus in every relation a much less morphological connection exists between larva and imago in the Muscids, than in the Tipulids, and in this fact is to be sought the reason for the relation of the duration of larval life to the long pupal stage.*

In *Sarcophaga* it requires eighteen days from the pupation to the exclusion of the fly, in *Corethra* only three. However, on the other hand the life of the larva of *Sarcophaga* lasts only eight days, in *Corethra* three or more weeks, and this difference cannot alone be referred to the wholly opposite mode of nourishment of the two larvæ, which makes it possible in the *Musca* larva to suffer a great mass of food to pass in a few days through its intestine, while the *Corethra* living by robbery only slowly procures food. The evidence lies in the very long interval, which separates the last moulting of the larva from the pupation in *Corethra*. It is surely not unimportant or adventitious, but will be met with in cases where the origination and completion of the appendages of the imago must take place within this period.

The pupa of *Corethra* manifestly differs in morphological as

* Evidently it is only the relative, not the absolute duration of the pupa-stage, which is here considered. This may vary in one and the same species between wide limits; for example the pupa-stage of *Corethra* lasts only three days in midsummer; in March the same lasts eight days. But also the corresponding life of the larva is longer in such March pupæ, the larvæ having wintered over from the preceding autumn. In the Muscidæ on the contrary, the pupa winters over.

well as physiological relations from the pupa of the Muscidæ; it does not *become* the imago, but it *is* nothing else from the start, and undergoes only a slight completion, in order to slip out from the pupa-skin as a winged and sexually mature insect. A pupa-sleep in the true sense it thus completely lacks, all functions of animal life in the pupa go on uninterruptedly, only the act of taking food ceases. All the occurrences which fill out the interval of latent life in *Musca*, during which the blood no more circulates, every sensation and movement, as well as the taking of food—every act which may go under the head of “formation of the pupa” fall in *Corethra* into the larval period, and the pupal stage is to be compared with the two last days of the Muscid pupa; when still in this respect the almost fully formed insect stands near its final perfection, since it, if artificially freed from its tun-shaped case, is more or less movable and lively.

Finally, we may distinguish two diametrically opposed forms of insect metamorphosis; the one represented by *Corethra* stands nearest to development without metamorphosis; the other represented by *Musca* is farthest removed from the ametabolic development and is the most extreme form of metamorphosis. Expressed in a very general way, the difference between the two consists in this, that at one time a *continuous*, at another a *discontinuous development* occurs, in the sense, namely, that the parts of the body and organs of one stage of development originate directly from the similar parts of the foregoing stage; or if such is not the case, rather the parts of the body and internal organs of the later stages of development are substantially new formations.

We may briefly characterize the two modes somewhat thus:—

Type *Corethra*. *The larval segments are converted directly into the corresponding divisions of the imago; the appendages of the head into the corresponding ones of the head of the imago; those of the thorax arise after the last moult of the larva, as outgrowths of the hypodermis around a nerve or trachea, from the cellular envelope of which the formation of tissue in the interior of the appendages issues. The larval muscles of the abdominal segments are transferred unchanged, into the imago; the thoracic muscles peculiar to the imago, as also some additional abdominal muscles, are developed in the last larval period from indifferent cellular filaments which are indicated even in the egg. The genital glands date back to the embryo, and are gradually developed; all the other systems of organs*

pass with little or no alteration into the imago. Fatty body none or inconsiderable. Pupa state short and active.

Type Musca. Thorax and head of the imago arising independently from the corresponding divisions of the hypodermis of the larva; only the abdomen directly through the transformation of the eight hinder larval segments. Thorax and head with their appendages develop from imaginal disks, which are of embryonal origin and are attached within the cavity of the body to nerves or tracheæ. Immediately after the formation of a tun-shaped pupa case from the chitinous skeleton of the larva, the imaginal disks grow together into the thorax and head. Destruction of all the systems of larval organs, either total or through histolysis. New formation of the same by means of the masses of nuclei arising out of the destruction of the fatty body. Genital glands indicated in the embryo have a continuous further development. Pupa state lasting for a long time and with a latent life.

The two types are most sharply distinguished from each other by the presence or absence of true imaginal disks, and I might for this reason suggest dividing those insects having a metamorphosis into *Insecta discota* and *adiscota*.*

A subsequent memoir remains to be prepared, in which an effective division is to be made showing what families belong to one and what to the other group. It may be here previously observed, that the two groups do not stand completely opposed, without transitions, but that there are intermediate forms; indeed whole families, perhaps whole orders of insects may on account of the want of imaginal disks be regarded as *Insecta adiscota*, while their development in other respects may closely join them to the *discota*.

*The italics in this translation are the author's.